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Relationships of mass properties and body proportions to locomotor habit in terrestrial Archosauria

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Abstract

Throughout their 250 Ma history, archosaurian reptiles have exhibited a wide array of body sizes, shapes and locomotor habits, especially in regard to terrestriality. These features make Archosauria a useful clade with which to study the interplay between body size, shape and locomotor behaviour, and how this interplay may have influenced locomotor evolution. Here, digital volumetric models of 80 taxa are used to explore how mass properties and body proportions relate to each other and locomotor posture in archosaurs. One-way, non-parametric, multivariate analysis of variance, based on the results of principal components analysis, shows that bipedal and quadrupedal archosaurs are largely distinguished from each other on the basis of just four anatomical parameters ($P < 0.001$): mass, centre of mass position and relative forelimb and hindlimb lengths. This facilitates the development of a quantitative predictive framework that can help assess gross locomotor posture in understudied or controversial taxa, such as the crocodile-line *Batrachotomus* (predicted quadruped) and *Postosuchus* (predicted biped). Compared to quadrupedal archosaurs, bipedal species tend to have relatively longer hindlimbs and a more caudally positioned whole-body centre of mass, and collectively exhibit greater variance in forelimb lengths. These patterns are interpreted to reflect differing biomechanical constraints acting on the archosaurian bauplan in bipedal *versus* quadrupedal groups, which may have shaped the evolutionary histories of their respective members.

Keywords

Archosaur; centre of mass; locomotion; biomechanics; digital modelling

Introduction

Archosauria (the 'ruling reptiles') is a diverse, long-lived (~250 Ma) saurian clade that dominated terrestrial, aquatic and aerial ecosystems throughout the Mesozoic Era, and persists to the present day in the form of about 23 crocodylian and 10,000 bird species (Jetz et al. 2012, Oaks 2011). Throughout their history, archosaurs have displayed disparate body plans and divergent locomotor habits, including obligate bipedal and quadrupedal species, as well as volant, semi-aquatic and marine forms (Fig. 1). The majority of archosaurs were land-dwelling, and it is well known that many important innovations related to terrestrial locomotion evolved throughout archosaur history (Bakker 1971, Charig 1972, Hutchinson 2006, Hutchinson and Gatesy 2000, Parrish 1986, Sullivan 2015). Terrestrial locomotor evolution in archosaurs is also characterized by repeated instances of morphological and functional convergence, involving members of both the ornithodiran (bird-line) and pseudosuchian (crocodile-line) lineages (Bates et al. 2012, Bates and Schachner 2012, Carrano 2000, Grinham et al. 2019, Kubo and Kubo 2012, Maidment and Barrett 2012, Nesbitt and Norell 2006, Parrish 1986, Sereno 1991, Walker 1964).

Given their long evolutionary history and diverse array of body sizes and shapes, terrestrial archosaurs provide a good case study by which to investigate how size and gross body proportions may relate to each other and locomotor behaviour. Yet, extant archosaur species occupy a very select subset of the total range of observed archosaur postcranial morphologies, and concomitantly exhibit disparate locomotor patterns that almost certainly do not capture the full range of historical diversity in archosaur locomotor behaviour (Hutchinson 2006, Hutchinson and Gatesy 2000). There is no archosaur — indeed, any animal — alive today that is of a comparable size and shape to extinct taxa like *Postosuchus* or *Iguanodon*. Although extant species may be highly useful for the development of 'lower

level inferences' such as soft tissue anatomy, their utility can become increasingly uncertain for 'higher level inferences' such as locomotor function and behaviour (Bates and Falkingham 2018, Hutchinson 2006, Witmer 1995). Thus, the usefulness of extant archosaur species as a basis for deriving broad inferences (grounded in homology or analogy) of locomotion for *all* extinct archosaurs is uncertain. Understanding locomotor habit in extinct archosaurs has therefore frequently relied on interpreting bony anatomy or footprints preserved in the fossil record. For instance, hoof-shaped manual unguals suggest at least some use of a quadrupedal stance (Maidment and Barrett 2014), and narrow-gauge footprints left by a single pair of feet may indicate at least intermittent parasagittal bipedalism (Thulborn 1990). The insights afforded by these lines of evidence can be important, but they are limited by the incompleteness of the fossil record (i.e., such evidence is only preserved for some species, and even then footprints can rarely be assigned to a known species), and perhaps more critically, they often cannot be generalized across large clades of disparate body plans.

An alternative approach to investigating locomotor patterns across a clade as morphologically diverse as Archosauria is one based on phenomena that affect all species in a universal fashion. For example, the manner of stance and gait of all archosaur species are (or were) fundamentally dictated by Newtonian mechanics, insofar as the size and proportions of any terrestrial animal greatly influence its ability to support and move its body on land. Body mass is paramount, as the mass that an animal must support against gravity increases more quickly with respect to size (e.g., length) than the cross-sectional area of supportive tissues such as muscle and bone (Alexander 1985, Biewener 1990, Campione and Evans 2012, Vogel 2003). Limb size, as well as intra- and inter-limb proportions, will dictate the range of possible kinematics such as stride length and patterns of inter-limb coordination (Alexander and Jayes 1983, Gatesy and Biewener 1991, Gatesy and Pollard

2011, Sellers et al. 2009), as well as potential locomotor performance (Carrano 1999, Garland and Janis 1993). The location of the whole-body centre of mass (COM), which represents the collective distribution of mass throughout the body, will also exert a strong influence on posture and movements. In order to maintain stability, an animal must keep its COM over the 'polygon of support' formed by its feet (however many) when standing (Alexander 2006, Winter 2009), and this principle can be extended to dynamically stable locomotion as well (Herr and Popovic 2008).

Many previous studies have estimated body mass or COM in extinct archosaurs through a variety of approaches, yet these have seldom been used in a comparative context to address broad questions concerning locomotor disparity or evolution (Allen et al. 2013, Bates et al. 2016, Henderson and Snively 2003). Here, previously published estimates of terrestrial archosaur mass properties and body proportions are synthesized with new computational models for additional taxa, spanning five orders of magnitude in mass and almost 250 Ma of evolution. The aims of the present study were twofold: to investigate how different aspects of body shape and size may or may not statistically relate to each other and gross locomotor habit (here taken to mean bipedal *versus* quadrupedal stance) in terrestrial Archosauria; and secondly, to develop a generalized and quantitative predictive framework that can be used to help assess locomotor habit in uncertain or enigmatic taxa.

Material and Methods

Computational Modelling

With the exception of the models of *Rapetosaurus* (Bates et al. 2016) and *Dreadnoughtus* (Lacovara et al. 2014), it was assumed here that the models used in the core component of

the present study were of adult (or near-adult) animals. Determining the ontogenetic status of many extinct archosaurs is not straightforward (Hone et al. 2016), but the models used consistently fell at or near the upper end of the known size range for each of the taxa studied, and were therefore assumed to represent 'adult' morphology. In terms of the anatomical parameters investigated (see below) and broad comparative approach of the study, it was felt that this assumption was justified, although the extremely limited number of known specimens for some taxa renders it difficult to test.

Previously published three-dimensional (3-D) digital volumetric models for 72 taxa were used (see Supplementary Material, Table S1), which includes two non-archosaur archosauriforms, six pseudosuchians (including two extant taxa), one non-dinosaur dinosauromorph, 15 ornithischians, 29 theropods (including five extant taxa) and 19 sauropodomorphs. These data were synthesized with new models for an additional eight taxa (one extant, seven extinct). For all the extinct taxa, and some of the extant taxa, digital volumetric models were produced using one of three established protocols (Fig. 2): a 3-D slicing method that discretizes the body into a series of elliptical frusta (Henderson 1999); a convex hull-based method whereby convex hulls are fitted around each major body segment (Bates et al. 2016, Sellers et al. 2012); and a spline- or hoop-based method whereby a series of polygonal hoops are fitted around each body segment and then lofted together (Allen et al. 2013, Allen et al. 2009). All three methods have been previously demonstrated to produce accurate results for a variety of extant tetrapod taxa (for which, admittedly, the approximate body geometry is already known).

Models for three extant avian taxa (*Gallus*, *Anas* and *Buteo*) were generated directly from computed tomographic scanning of whole carcasses (*Gallus*: Allen et al. 2013, *Anas* and *Buteo*: Macaulay et al. 2017), and the values for mass and centre of mass (COM) location

used for these models were taken from the 'best guess' results; see Allen et al. (2013) and Macaulay et al. (2017) for details on density assignment. The same approach was also used to generate the new model of *Crocodylus moreletii* (machine tube voltage 120 kV, tube current 233 mA, exposure 750 ms, pixel resolution 0.977 mm, slice thickness 1.5 mm; scan segmentation in Mimics 19.0 (Materialize NV, Leuven, Belgium)), with density assignments following 'best guess' values of Allen et al. (2013) and Macaulay et al. (2017). For most other models, the values for mass and COM in all other models were taken directly from the original, published results. Two exceptions to this were as follows:

1. For the theropod models of Allen et al. (2013), a 'best guess' model did not exist, but rather there were endmember extremes used to delimit the plausible ranges of mass and COM in the original study. In the present study, the mass used was the average of the 'maximal mass' and 'minimal mass' models, and the COM location used was the average of the 'maximally cranial' and 'maximally caudal' models.
2. For the sauropodomorph models of Bates et al. (2016), mass and COM were determined following an approach that differed slightly to the original study. Low-density (e.g., lung) volumes were ignored, and rather the '+21%' convex hull models for all segments were used to calculate segment mass properties directly, assuming a density of 1,000 kg/m^3 for the tail and limbs and a density of 850 kg/m^3 for the trunk, neck and head. The purpose of this alternative protocol was to enable total consistency with new models that were generated in this study via the convex hull technique (detailed below).

Seven new extinct taxa were added to the present study, and were generated as follows. *Tenontosaurus*, *Trilophosaurus*, *Stenaulorhynchus* and *Protoceratops* were modelled using the convex hull method as described above for the sauropodomorphs of Bates et al. (2016), based on digital skeletal geometries previously published by Clauss et al. (2017). *Edmontonia* was also modelled using the same convex hull method, but this was based on a digital skeletal

sculpt based on fossil material (www.animalsimulation.org). *Batrachotomus* and *Muttaburrasaurus* were modelled using the spline-based method, and were based on digital skeletons generated from photogrammetry of mounted skeletons (*Batrachotomus*: Staatliches Museum für Naturkunde, Stuttgart; *Muttaburrasaurus*: Queensland Museum, Brisbane), using the software Agisoft Photoscan 1.04 (Agisoft LLC, Russia). The lungs of both taxa were modelled as filling the cranial portion (cranial half in the 'maximally caudal' model, cranial quarter in the 'maximally cranial' model) of the thoracic cavity (Allen et al. 2013, Allen et al. 2009); no abdominal or other air sacs were modelled owing to the paucity of evidence for postcranial skeletal pneumaticity in pseudosuchians and ornithischians (Butler et al. 2012).

Comparison of Modelling Methods

Previous studies that have used digital volumetric modelling of extinct taxa have typically employed only a single modelling protocol, whereas the current study draws upon data from three. In addition to technical details concerning model generation and density assignment, there are at least three important differences between the methods involved:

1. Whereas the convex hull and spline-based methods are based on 3-D digital skeletal reconstructions, the 3-D slicing method is based on two-dimensional reconstructions (lateral and dorsal views).
2. Both the convex hull and spline-based methods create models in a standard posture, with the forelimbs either held out held out directly laterally or ventrally from the body, and the hindlimbs directed downward (Fig. 2C); often the vertebral column is also held in a straightened fashion for at least part of its length. In contrast, models generated using the 3-D slicing method have a more natural, life-like pose, but one that is not necessarily standardized across models.

3. Both the 3-D slicing and spline-based methods involve a significant element of manual investigator input in the generation of (albeit more natural) flesh contours, whereas the convex hull method is almost entirely automated. Nonetheless, in the spline-based method of Allen et al. (2009), the contours are based on empirically-derived scaling factors, regarding how 'inflated' contour cross-sections are with respect to the underlying skeleton; it hence lies between the 3-D slicing and convex hull methods in terms of objectivity.

The collective differences between the three approaches raise the possibility that there may exist one or more systematic differences in estimates of mass or COM location between the modelling methods.

As the comparability of different protocols' results has yet to be formally examined, an attempt was made here to assess method consistency. This assessment was unfortunately restricted by the strong historical bias between methodology and locomotor habit in the current dataset (chi-square test for association, $\chi^2 = 30.5$, $P < 0.001$; Table S1); for instance, of the taxa with 'known' locomotor habit (see below), only one quadruped was modelled using the spline method. Moreover, there was also strong bias between methodology and clade ($\chi^2 = 56.2$, $P < 0.001$; Table S1). Such bias not only limits the ability to distinguish systematic differences between modelling methods from genuine differences due to locomotor habit or clade, but it also limits the ability to delimit the true nature of any such difference between methods and thence apply appropriate corrections to the dataset (e.g., corrections may be disproportionately applied to some locomotor habits or clades). Here, estimates for mass and COM location for 27 taxa that had been modelled using multiple protocols were compiled, using both previously published results and new models generated here via 3-D slicing or convex hulling (see Supplementary Material, Table S2). Generation of convex hull models followed the same protocol as outlined above. Not all 27 taxa were

modelled using all three methods, but in each case at least two had been used. As different-sized skeletons were often used as the basis upon which these models were built, the attempt was made to first remove the effect of size by normalizing the estimates of mass and COM location (distance cranial to the hips) by glenoacetabular distance (GA):

$$\text{mass}^* = \frac{\sqrt[3]{\text{mass}}}{\text{GA}} \quad (1)$$

$$\text{COM}^* = \frac{\text{COM}}{\text{GA}} \quad (2)$$

Whilst the normalization expressed in equation 1 assumes isometry, it is important to recognize that the normalized values were only compared vis-à-vis for (at worst) slightly different-sized models of the same taxon. They were not compared across models (taxa) of widely varying sizes or proportions, for which the assumption of isometry is clearly untenable. Given that within a taxon there would be relatively little scope for size differences to begin with (indeed, in some cases, the same underlying skeleton was used for multiple methods), the assumption of isometry being violated here was considered negligible.

For a given pair of methods, normalized values of mass and COM location were compared using the 'smatr' package (v 3.4-3; Warton et al. 2012) in R 3.5.2 (R Core Team 2012). A major-axis (MA) regression forced through the origin was fit to the data, and then tested for whether its slope was statistically different from 1.0 (significance level set at 0.05); if there was a difference, this suggested that one method tended to systematically under- or overestimate a given parameter compared to the other. The use of a zero-intercept MA regression here was simply to test the congruence between a given pair of methods, such that the MA slope gives a measure of systematic deviation. This assumed that if there was a systematic difference in one method compared to another, that difference would be proportional to the magnitude of the quantity being compared; given the manner in which the

digital models were constructed, it was considered implausible that a negative-slope (or non-zero intercept) relationship could occur between two methods.

Regression indicated that some systematic differences did indeed exist, as far as can be determined with the current sample (Table 1). The convex hull method gave different estimates from the spline method in terms of both COM and mass, and from the 3-D slicing method in terms of COM; yet there was no detectable difference between 3-D slicing and spline methods. Assuming that these differences also extended to the main dataset, values for mass and COM derived from the convex hull method in the main dataset were 'normalized' with respect to the spline method (Table S1), using the MA regression slopes as correction factors:

$$\text{mass}_{\text{spline-corrected}} = \frac{\text{mass}_{\text{convex hull}}}{0.90717^3} \quad (3)$$

$$\text{COM}_{\text{spline-corrected}} = \frac{\text{COM}_{\text{convex hull}}}{1.5434} \quad (4)$$

This restricted analysis of, and correction for, systematic difference between modelling methods is admittedly weak, and consequently in all remaining analyses statistical significance was conservatively identified with an alpha level of 0.01. Evidently, the issue deserves a more thorough and rigorous investigation in the future, which will first require the generation of many more models to reduce the aforementioned distribution biases. Until such detailed investigation is undertaken, it is prudent that future studies that focus on a single taxon should employ multiple methods (e.g., Otero et al. 2019) as a way of assessing the sensitivity of the results to the modelling method used.

283 ***Parameters Investigated***

284 For each model, four anatomical parameters were determined, in addition to GA (Fig. 2D):
285 body mass (BM), COM location cranial to the hips (COM_X), hindlimb length (HL) and
286 forelimb length (FL). The use of these four relatively simple parameters is justified on the
287 basis that each has direct physical relevance to terrestrial locomotor biomechanics (see
288 Introduction section above). It is worth re-iterating here that only volumetric models were
289 used in this study as they give internally consistent, and mechanistically based, estimates of
290 both BM and COM_X, in contrast to other methods that compute BM only, such as those
291 based on propodial minimal circumferences (e.g., Campione et al. 2014). Such mechanistic
292 estimates in turn can be more lucidly related to other aspects of locomotor biomechanics.
293
294 Due to the vast range in absolute size across the taxa sampled, the raw values for each
295 parameter were corrected to account for differences in size. For BM, the base-10 logarithm
296 was taken, which also helped reduce the sample distribution's skewness. For the linear
297 metrics of COM_X, HL and FL, a linear regression of each metric against GA was computed
298 in R and residuals were extracted; to account for suspected differences in allometric
299 trajectories between GA and the different metrics, the base-10 logarithm of each metric was
300 taken first before computing the regressions. This use of residuals was favoured over the
301 computation of basic ratios (e.g., HL/GA) as it reduces heteroscedasticity and nonlinearity in
302 the resulting dataset.
303
304 In the original dataset, the archosauromorph *Trilophosaurus* had a negative COM_X position
305 (Table S1), caused at least in part by its long and proximally deep tail, which is
306 incompatible with the above approach of computing logarithms. The long tail would
307 presumably have been dragged on the ground in life for some of its length (Gregory 1945),
308 and this would have shifted the COM of that part of the body supported by the limbs to lying

cranial to the hips by some amount. As such, COM of this taxon was nominally set as 1 cm cranial to the hips. Given that *Trilophosaurus* is the most stemward taxon in the current dataset, this was judged as an acceptable modification to facilitate statistical analysis.

Statistical Analyses

Phylogenetically informed statistical analyses of the size-corrected anatomical variables were conducted in R using a fully resolved, time-calibrated phylogenetic tree of the study taxa, which follows the 'traditional' hypothesis of dinosaur interrelationships (see Supplementary Material, Fig. S1). The topology of the tree was based on Nesbitt (2011) and Ezcurra (2016) for Archosauromorpha and Pseudosuchia, Carrano and Sampson (2008), Carrano et al. (2012), Jetz et al. (2012), Allen et al. (2013) and Loewen et al. (2013) for Theropoda, Nair and Salisbury (2012), Otero and Pol (2013), Tschopp et al. (2015) and Bates et al. (2016) for Sauropodomorpha and Butler et al. (2007), Prieto-Márquez (2010), Butler et al. (2011), McDonald (2012) and Farke et al. (2014) for Ornithischia. The ages used for terminal taxa and internal nodes for this tree are reported in Supplementary Tables S3 and S4, respectively. Analyses were also conducted using a second tree of markedly different topology, based on the 'Ornithoscelida hypothesis' of dinosaur interrelationships (Baron et al. 2017; see Supplementary Material, Fig. S2); the ages of terminal taxa remained identical to that of the first tree, whereas the ages used for the internal nodes are reported in Supplementary Table S5.

Phylogenetic principal components analysis (pPCA; Revell 2009) was used to explore how morphological variation related to locomotor habit, using the 'phytools' package for R (v 0.6; Revell 2012), where the evolutionary correlation matrix was derived assuming a Brownian model of trait evolution. To assess the influence of phylogeny, the *K* statistic (and

associated *P* value) of Blomberg et al. (2003) was also determined in phytools. In this study, the locomotor habit of each taxon was classified *a priori* based on current consensus (see also Grinham et al. 2019, Maidment and Barrett 2014, Thulborn 1990, and references cited therein), as either obligate biped ($n = 33$), obligate quadruped ($n = 34$) or 'other' ($n = 13$), where the last category contained taxa hypothesized to be facultatively bipedal, or taxa whose habits are controversial or previously not assessed in detail. Locomotor mode is here defined as the stance adopted during straight-line, level, quasi-steady walking.

The pPCA served primarily as an aid to qualitatively assess broad patterns. The distinction between bipedal and quadrupedal principal component (PC) scores was quantitatively tested with a one-way, non-parametric, multivariate analysis of variance (PERMANOVA) in the 'vegan' package for R (v 2.5-6; Oksanen et al. 2019). Disparity in PC scores was estimated for bipeds and quadrupeds using Procrustes distance regression in the 'geomorph' package in R (v 3.1.1; Adams et al. 2018). To investigate how the size-corrected anatomical parameters themselves related to each other and locomotor habit, three analyses were undertaken. Firstly, a phylogenetic multivariate analysis of variance (pMANOVA) was conducted, using phylogenetic Procrustes distance regression, to test if there was an overall difference between bipeds and quadrupeds considering all four parameters together. Secondly, a phylogenetic analysis of variance (pANOVA) was conducted using the phytools package, to test if there was a difference between bipeds and quadrupeds considering each parameter independently. Lastly, pairwise comparisons between parameters were conducted for bipeds and quadrupeds via MA regression, using the smatr package. This involved correcting the values for each parameter for phylogenetic signal, using phylogenetic generalized least squares in the 'caper' package in R (v 0.5.2; Orme et al. 2015), the residuals from which were then used in the regressions. The slopes for a given pairwise MA fit were compared between bipedal and quadrupedal taxa using the smatr package.

361

362

363 ***Predictive Framework***

364 Linear discriminant analysis (LDA) was used to produce a predictive framework for
365 archosaur locomotor mode based on the original (size-corrected) anatomical parameters,
366 using the 'MASS' package for R (v 7.3-50; Venables and Ripley 2002). Instead of deriving
367 a single predictive model, 11 variants were tested here, which differed in the combination of
368 anatomical variables (two, three or all four) used in the training dataset. In addition, as birds
369 were found to occupy a distinct position in morphospace (see Results below), two variants
370 of the training dataset were also tested: one with all 'known' taxa (i.e., 33 bipeds and 33
371 quadrupeds) and one excluding birds (i.e., 25 bipeds and 33 quadrupeds); as *Trilophosaurus*
372 was found to be a morphological outlier (see Results below), it was excluded from both
373 training datasets. Hence, a total of 22 different training datasets were tested to identify which
374 resulted in predictions most consistent with the postures assigned to 'known' bipeds and
375 quadrupeds (see Supplementary Material, Table S6). The consistency of each LDA with pre-
376 defined assignments for 'known' taxa was assessed using leave-one-out testing (jackknifing)
377 of the training dataset and computing the total success rate. Subsequently, each LDA was
378 then used to predict locomotor habit for the 'other' taxa, for which locomotor habit is
379 currently uncertain or controversial. It is worth noting that LDA will always classify a given
380 subject into one of the available categories, regardless of how congruous it actually is with
381 other data in the same category.

382

383 Initial analyses with additional models suggested that LDA may produce spurious results for
384 immature specimens with morphologies (or even stance) that are qualitatively different from
385 those of adults. As such, in addition to the original 13 'other' taxa used in the above
386 statistical analysis, two previously published models were included to explore the relevance

of the LDA for assessing ontogenetic effects on locomotor mode: a juvenile *Alligator* (Bates et al. 2016) and a hatchling *Mussaurus* (Otero et al. 2019).

Monte Carlo Simulation

Two of the primary variables used in this study, BM and COM_X, are estimates derived from computational volumetric models; as estimates they may therefore carry an attendant level of error from the 'true' value (were it ever able to be known). In turn, error in the baseline dataset may affect the results obtained and the conclusions drawn from them. To explore the effect of error in BM and COM_X estimates, a Monte Carlo simulation was performed with 1,000 replicates, wherein BM and COM_X was allowed to randomly vary up to a prescribed amount, and the pPCA and LDA were re-computed. Based on the results of Henderson (1999) and Allen et al. (2009), both BM and COM_X were allowed to vary by up to ±15% of their original values.

Results

Patterns of Anatomical Variation

The results of pPCA differed only marginally between the two phylogenies used (traditional *versus* Ornithoscelida hypotheses of dinosaur interrelationships). Comparison of the PC scores between the two trees using symmetric Procrustes superimposition in the vegan package showed that the score sets were not significantly different (multivariate correlation coefficient = 0.999, $P < 0.001$). Moreover, the relative difference between PC scores for a given taxon between the two phylogenetic hypotheses was on average 0.015% for PC1, 0.357% for PC2, 0.148% for PC3 and 0.370% for PC4; that is, the score a given taxon

received on average differed by <1% between the two phylogenies used. Therefore, only the results derived from using the traditional phylogeny are presented herein. Despite the minimal difference in pPCA results between the two tree topologies, three of the four anatomical parameters showed a low to modest influence of phylogeny (BM: $K = 0.57$, $P = 0.001$; HL: $K = 1.11$, $P = 0.001$; FL: $K = 0.39$, $P = 0.001$). This indicated that the phylogenetic effect originated from at least one crownward part of the tree; since the difference between the two trees used occurred very deep within the phylogeny, the scope for phylogenetic effects in more crownward parts remained unaltered.

Each PC was loaded moderately to strongly by at least two anatomical parameters (Table 2); PC1 accounted for 47.47% of the total data variance, PC2 accounted for 25.61%, PC3 accounted for 19.4% and PC4 accounted for 7.52% of the total variance. There was a very strong distinction between bipedal and quadrupedal taxa in PC space, both visually (Fig. 3, Supplementary Material, Movie S1) and as indicated by PERMANOVA ($F_{1,65} = 16.25$, $P < 0.001$). Some of the 13 'other' taxa tended to bridge between the bipedal and quadrupedal morphospaces in PC space, often plotting near the region of overlap between the two morphospaces, whereas others plotted either within one particular morphospace or outside of both (Fig. 3, Supplementary Material, Movie S1). Birds (except the giant, flightless *Struthio*) occupied their own distinct region of the bipedal morphospace, characterized by the lowest (most negative) PC3 values; comparably low values were not present in any quadruped. *Trilophosaurus* was an outlier for the quadrupedal morphospace, its position in PC space — closer to bipeds than quadrupeds — being driven heavily by its caudal COM_X position (Fig. 3, Supplementary Material, Movie S1).

Procrustes disparity of the bipedal morphospace of PC scores was not significantly different from that of the quadrupeds (108.7 *versus* 92.2, respectively; $P = 0.49$), a result that

remained unaltered when *Trilophosaurus* was excluded from consideration. Distilling this down to each PC, however, it was apparent that there were marked differences between bipeds and quadrupeds (Table 3). Quadrupeds showed more than double the variation in PC1 than bipeds, a result that appears to have been driven in large part by ornithischians. Conversely, bipeds showed more than six times the variation in PC3 than quadrupeds, a result that probably stemmed in large part from the high variance in theropods (including birds), given that theropods comprise the majority of bipeds in the current sample. Indeed, PC3 was loaded most strongly by BM and COM_X (Table 2), two parameters for which phylogenetically directed trends within Theropoda have been previously noted (Allen et al. 2013, Benson et al. 2018, Lee et al. 2014, Turner et al. 2007). Bipedal and quadrupedal morphospaces were well (but not completely) separated along the PC2 axis (Fig. 3, Supplementary Material, Movie S1), which was mostly loaded by COM_X and hindlimb length (Table 2); this suggests that, broadly speaking, bipedal archosaurs have longer hindlimbs and a COM_X located closer to the hips.

In terms of the anatomical parameters themselves, pANOVA indicated that bipeds and quadrupeds were statistically indistinct when each parameter was considered separately (cf. Table 4). However, more holistically, pMANOVA of the anatomical parameters showed that bipeds were distinct from quadrupeds ($F_{1,65} = 44.74$, $r^2 = 0.41$, $P < 0.001$), and were almost twice as disparate morphologically than quadrupeds (Procrustes variances of 2.38 and 1.22, respectively; $P = 0.005$). Bipeds displayed more than double the variance in BM than quadrupeds, a result again strongly driven by theropods (Table 4), whose range in absolute values of BM in the current dataset spans more than five orders of magnitude (compared to a little over three orders of magnitude across all quadrupeds).

464 The results for all pairwise comparisons of phylogenetically corrected anatomical values are
465 reported in Table 5, and pairwise plots of phylogenetically reduced residuals are presented in
466 Fig. 4. In both bipeds and quadrupeds, FL was significantly and positively correlated with
467 HL, although the relationships were statistically indistinguishable between the two groups;
468 furthermore, it cannot be discounted that these results are not partly driven by spurious
469 correlation with glenoacetabular distance, as both variables were normalized with respect to
470 this distance in deriving residuals. In addition, FL was significantly and positively correlated
471 to COM_X in bipeds; that is, a relatively more cranial COM location was tied to relatively
472 longer forelimbs (cf. Allen et al. 2013). Unconventionally, COM_X and BM were found to be
473 positively correlated in bipeds, but the significance of this trend was driven solely by the
474 outlying residuals for *Heterodontosaurus* (Fig. 4).
475
476
477 ***Linear Discriminant Analysis***
478 Of the 22 variants in LDA tested, three of the four best-performing variants excluded birds
479 from the training dataset, and had success rates exceeding 98% (Supplementary Table S6).
480 Indeed, excluding birds from the training dataset almost always resulted in an improvement
481 in classification success rate. The single best LDA used COM_X + HL + FL ('model 21') as
482 the combination of anatomical variables in the training dataset, with a classification success
483 rate of 100% (Supplementary Table S6). Typically, the assignment of the training dataset
484 taxa into bipedal or quadrupedal categories was relatively unambiguous; for instance, in
485 'model 21', more than 80% of the training taxa had posterior probabilities exceeding 0.95.
486 These results further affirmed the strong distinction between bipeds and quadrupeds in the
487 current sample. The most frequently misclassified training dataset taxa were the
488 pseudosuchian *Riojasuchus* (misclassified as bipedal, 12 out of 22 times) and the sauropod
489 *Neuquensaurus* (misclassified as bipedal, 11 out of 22 times), which had COM_X residuals

among the lowest, if not the lowest, values for their respective clades (i.e., caudal COM_X location), potentially explaining their relatively frequent misclassifications. Both taxa are known from the majority of the skeleton (Otero 2010, von Baczko et al. in press), suggesting underlying causes other than reconstruction error, such as apomorphic anatomies. For instance, *Neuquensaurus* was quite small for a sauropod, and moreover it possessed a very broad pelvis, potentially resulting in a more caudal COM_X location.

The classifications assigned to the 15 'other' taxa for the four best-performing models are reported in Table 6. The classifications broadly corresponded to qualitative observations of how each taxon plots in PC space (Fig. 3, Supplementary Movie S1). As an explicit 'facultatively bipedal' category was not included, the posterior probabilities determined may give some tentative indication of how often bipedalism and quadrupedalism were used during normal activity. The pseudosuchians *Postosuchus* and *Batrachotomus* were strongly supported as a biped and quadruped, respectively. The enigmatic archosauriform *Euparkeria* was also classified as a quadruped, although in PC space it plotted well clear of the bipedal and quadrupedal morphospace and hence this result should be viewed with caution. In general concordance with a recent study (Otero et al. 2019), adult *Mussaurus* was frequently classified as a biped, whereas its hatchling was frequently classified as a quadruped (including in the best-performing model). The juvenile *Alligator* model was frequently (mis)classified as a biped (73% of LDA variants), whereas the jackknifed classifications of the adult *Crocodylus* models (quadrupedal) were frequently correct (70% of LDA variants).

Monte Carlo Simulation

Simulation indicated that the results of pPCA were very robust to error in BM and COM_X. Of the 1,000 replicates, not one resulted in a set of PC scores that was significantly different

from (i.e., uncorrelated with) the scores obtained in the main analysis using the original estimates, as indicated by symmetric Procrustes superimposition ($P < 0.001$). The first three PCs still accounted for 92% of the dataset's variation on average (mean ± s.d. for each PC: PC1 = 47.1 ± 2.2%, PC2 = 25.9 ± 1%, PC3 = 19.4 ± 2.3%, PC4 = 7.6 ± 0.4%). The average direction of the loading vectors across the 1,000 replicates was within 5° of the original directions in the main analysis, and the angular standard deviation of the loading vectors' directions in PC1–3 space was 17° or less, indicating a narrow or acute 'cone of variation' (cf. Fig. 3). Procrustes disparity (104.7 ± 3.5 for bipeds and 90.9 ± 3.1 for quadrupeds, $P > 0.5$) and PERMANOVA results ($F_{1,65} = 15.8 \pm 0.6$, $P < 0.001$) also did not differ significantly from the results of the main analysis.

In terms of the LDA, model 21 remained the best-performing combination of anatomical variables, with a classification success rate of 98.53 ± 1.33 %. The distribution of posterior probabilities for classification of the 15 'other' taxa were also highly consistent with the original probabilities obtained in the main analyses; Fig. 5 illustrates the distributions for the model 21 combination. Nonetheless, the spread of probabilities for the juvenile *Alligator* and *Marasuchus* encompassed a considerable proportion of quadrupedal classifications; suggesting that the main analysis' classifications for these two taxa should be viewed tentatively.

Discussion

Patterns of Anatomical Variation

By synthesizing data derived from 3-D computational models, this study principally sought to examine how mass properties and gross body proportions relate to each other and

locomotor habit — here taken to mean bipedal *versus* quadrupedal stance — in terrestrial archosaurs. The results of pPCA indicated that, despite concerns regarding methodological bias in generating estimates, or potential error associated with this, bipedal and quadrupedal species were largely distinct from each other in morphospace (Fig. 3). Procrustes distance regression of all the original anatomical parameters themselves also recognized a clear distinction between the two groups. Yet, few differences existed between bipeds and quadrupeds on an individual parameter-by-parameter basis (Table 4), and no PC was loaded primarily by just one anatomical parameter (Table 2). These findings highlight how a holistic, multivariate approach can facilitate more rigorous, quantitative assessment of locomotor habit in extinct archosaurs.

Following on from this, the single clearest distinction between bipedal and quadrupedal taxa revealed in the present study was bivariate (Fig. 3, Supplementary Material, Movie S1): overall, bipeds have relatively longer hindlimbs than quadrupeds (paralleling the finding of Kubo and Kubo 2012), *and* have a COM located closer to the hips. This result is hardly surprising, as biological and mechanical intuition would lead to an expectation of this pattern. From a biological perspective, longer hindlimbs reflect greater investment of biomass in them as locomotive organs, and therefore likely reflect greater reliance on the hindlimbs during daily activity. From a mechanical perspective, the COM must be kept over a 'polygon of support' formed by the feet during static and dynamic activities (Alexander 2006, Herr and Popovic 2008, Winter 2009), the size of which is more restricted — and posteriorly positioned — in a biped. The size and mobility of the hindlimbs therefore constrains how far the COM is able to be located cranial to the hips in a biped (Gatesy et al. 2009, Hutchinson 2006), although postural differences can also modulate this relationship, as occurs in birds (Allen et al. 2013, Hutchinson and Allen 2009).

568

569 Quadrupedal archosaurs are (or were) probably also subject to their own form of locomotor
570 constraint. Compared to bipeds, the current sample of quadrupeds exhibited substantially
571 less variance in FL, and a similar variance in HL (Table 4), suggesting that in order to
572 coordinate stable, efficient progression, the dimensions of the limbs and intervening trunk in
573 quadrupeds need to be more closely coupled with one another (see also Thulborn 1982). The
574 adoption of bipedality and removal of this constraint can therefore enable uncoupling of
575 fore- and hindlimb locomotor modules (Gatesy and Dial 1996) and in turn promote greater
576 evolutionary variability in limb size. This raises a possible evolutionary scenario within
577 bipedal archosaurs, whereby relaxation of the 'coupled proportions' constraint may have
578 facilitated greater anatomical, functional and perhaps ecological innovation, which in turn
579 may have expedited the diversification of bipedal archosaurs across the Triassic–Jurassic
580 boundary and into the later Mesozoic. For example, constraint relaxation should have been
581 conferred by bipedality in the immediate ancestors of dinosaurs (Grinham et al. 2019). Such
582 relaxation would then have presaged the uncoupling of forelimb and hindlimb allometries at
583 the origin of birds, in association with the acquisition of powered flight (Dececchi and
584 Larsson 2013), which subsequently lead to phenotypic release in both limbs and increased
585 rates of evolution in stem birds (Benson and Choiniere 2013).

586

587 ***Predicting Locomotion in Extinct Archosaurs***

588 A secondary aim of this study was to develop a quantitative framework that could be used to
589 help predict locomotor habit in extinct terrestrial archosaurs, and that bipeds and quadrupeds
590 were largely distinct in PC space has facilitated this. Although beyond the scope of the
591 present study, this new framework has the potential to provide new rigour to assessments of
592 locomotor evolution within Archosauria, such as the frequency and phyletic distribution of
593 shifts from quadrupedalism to bipedalism (facultative and obligate; Chapelle et al. 2019,

Grinham et al. 2019, Kubo and Kubo 2012, McPhee et al. 2018). This would first require the generation of digital volumetric models for additional taxa, particularly those surrounding inferred transitions, which can be a non-trivial and time-intensive process.

Interestingly, it was found that excluding birds from the training dataset almost always resulted in improved classification accuracy. Birds occupied a distinct region of PC space in the current study, with strongly negative values along PC3 reflecting their overall smaller BM (compared to both bipeds and quadrupeds), and to a lesser extent their more cranial COM_X (compared to bipeds). It is possible that the tendency towards a more cranial COM_X makes birds more quadruped-like than most other non-avian bipedal archosaurs, impeding the ability of LDA to accurately separate out the two locomotor categories. As most birds are volant, and therefore not strictly terrestrial in their locomotor habit, the current study's findings echo previous arguments that birds are not a good candidate as modern analogues for studying locomotion in Archosauria as a whole (e.g., Carrano 1998, Gatesy and Middleton 1997, Hutchinson and Gatesy 2000).

Many of the predictions of the best performing LDAs in the current study concur with previous assessments, such as quadrupedality in *Batrachotomus* (Gower and Schoch 2009) and *Iguanodon* (Norman 1980), bipedality in *Lufengosaurus* (Bates et al. 2016, McPhee et al. 2018) and *Postosuchus* (Weinbaum 2013), and bipedality in adult *Mussaurus* but quadrupedality in its hatchlings (Otero et al. 2017, Otero et al. 2019). There are also conflicts with previous assessments, most notably the hadrosaurids *Gryposaurus* and *Edmontosaurus* being consistently classified here as bipeds. This is in contrast with the quadrupedal classification obtained for a third hadrosaurid, *Lambeosaurus*, despite the fact that all three taxa possess numerous osteological features suggestive of the use of quadrupedal stance (Dilkes 2001, Maidment and Barrett 2014), and reflected by many Late

620 Cretaceous quadrupedal trackways attributed to hadrosaurids generally (Lockley and Wright
621 2001). What, then, might explain this discrepancy?
622
623 The discord surrounding hadrosaurids has been noted previously: on the basis of propodial
624 proportions, the method of McPhee et al. (2018) was observed to have some difficulty with
625 quadrupedal taxa that possess biped-like humeral proportions. Hadrosaurids tend to have
626 gracile, 'biped-like' forelimbs, and this may be responsible for the (potential)
627 misclassifications obtained in the present study as well, which only used gross body
628 proportions as a basis for classifications. In future studies, it would be worthwhile to
629 combine the metrics used in the current study with those used by others, such as the
630 proportions of individual limb bones (McPhee et al. 2018) or the vertebral column (Christian
631 and Preuschoft 1996), into a single framework. Moreover, as discrete osteological features
632 have also frequently aided interpretations of locomotor habit (e.g., Maidment and Barrett
633 2014, Mallison 2010, VanBuren and Bonnan 2013), it would also be interesting to
634 incorporate such discrete measures into a quantitative predictive framework.
635
636 One further misclassification of the LDAs was that the juvenile *Alligator* model was often
637 misclassified as bipedal, yet there is no evidence of sustained, habitual or facultative
638 bipedalism in any extant Crocodylia. This result parallels a bipedal misclassification
639 obtained for a juvenile *Caiman* by McPhee et al. (2018). It is known that extant crocodylians
640 undergo substantial changes through ontogeny, in both cranial and postcranial proportions
641 (Allen et al. 2009, Dodson 1975, Iijima and Kubo 2019). Ontogenetic effects may therefore
642 distort relationships between individual bone proportions and mass, COM_X or other
643 posturally relevant parameters (e.g., see Brassey et al. 2015). The present study did not aim
644 to explicitly account for ontogenetic effects, and yet as noted above, the LDAs frequently
645 detected an ontogenetic shift in locomotor mode in the early sauropodomorph *Mussaurus*,

concordant with the interpretation of Otero et al. (2019). Whilst the same computational models were used in the present study and that of Otero et al. (2019), they were analysed and interpreted differently (one mechanistically, the other statistically), such that the consilience of interpretations further supports a shift in locomotor mode as *Mussaurus* matured. Ontogenetic changes in locomotor mode have been proposed for other extinct terrestrial archosaurs (e.g., Chapelle et al. 2019, Dilkes 2001, Heinrich et al. 1993, Słowiak et al. 2019, Zhao et al. 2013), and it would be interesting to explore the applicability of the current study's approach to testing these interpretations in the future.

Conclusion

By considering multiple parameters that describe whole-body mass properties and proportions, bipedal and quadrupedal archosaur taxa were largely distinguished from each other. The results presented here should nevertheless be viewed tentatively, as it remains to be fully determined how methodological differences (in deriving estimates of BM and COM_X) may influence the nature of the resulting comparative dataset, and hence any of the findings and interpretations made here. It is also important to recognize that the present study's dataset is biased towards two principal clades (Theropoda and Sauropodomorpha), and future sampling of additional disparate taxa (e.g., bipedal poposaurs, basal marginocephalians and long-legged crocodylomorphs or silesaurids) may potentially reduce the degree of distinction between bipedal and quadrupedal taxa. Furthermore, the mean body mass of the present study's taxa was 3393 kg, with more than half being >200 kg, and greater sampling of small-bodied taxa could enrich insights on the relationships between body form, size and locomotor habit. Despite these limitations, it is clear that a more holistic approach is required to fully understand locomotor behaviour and evolution within

672 archosaurs. Additionally, the findings of the present study suggest that important
673 biomechanical constraints on the bauplan of archosaurs (limb and trunk proportions)
674 influenced the scope and extent of anatomical variation in both bipedal and quadrupedal
675 species over their 250 Ma history.
676
677

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687
688

689 Author contributions

690

691 P.J.B., V.R.A. and J.R.H. conceived study design; P.J.B., K.T.B., V.R.A., D.M.H. and
692 J.R.H. produced digital models and contributed data; P.J.B. and M. R. conducted statistical
693 analyses; all authors contributed to results interpretation and writing the manuscript.
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695
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Competing interests

None.

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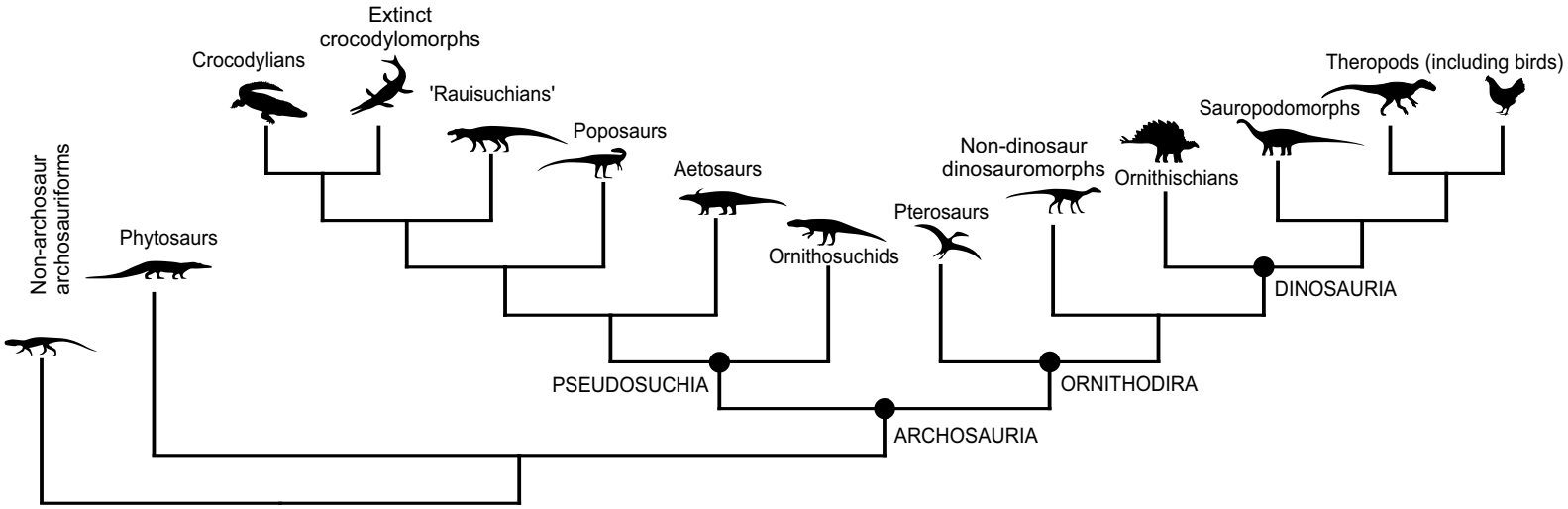
Figure captions

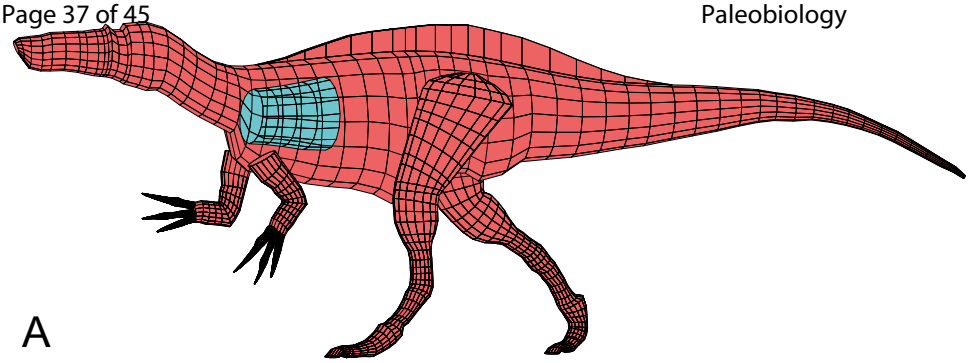
Figure 1. Simplified phylogeny of Archosauria based on current consensus of interrelationships (e.g., Ezcurra 2016, Nesbitt 2011), illustrating the diversity of body forms and locomotor habits across the group. Major clades are also indicated.

Figure 2. Digital modelling of extinct archosaurs. (A) 3-D slicing method, here with the theropod *Suchomimus*. (B) Convex hull method, here with the sauropod *Giraffatitan*. (C) Spline- or hoop-based method, here with the rauisuchian *Batrachotomus* (new analysis). Whereas 3-D slicing is based on two-dimensional illustrations in different views, the other methods are based on mounted skeletal material. In A and C, red denotes flesh and blue denotes air spaces (e.g., lungs). (D) Anatomical parameters extracted from each model used

959 in the analyses. Glenoacetabular distance was measured parallel to the sagittal plane, and
960 forelimb and hindlimb lengths were the sum of the lengths of the respective propdia,
961 stylopodia and metapodia (or their corresponding flesh segments).
962
963
964 **Figure 3.** 3-D plot of the first three PC scores for each taxon, which collectively accounted
965 for 92.5% of the variation in the dataset. The regions of space occupied by bipedal and
966 quadrupedal taxa are delimited by convex hulls (generated using Meshlab 1.3.3;
967 http://meshlab.sourceforge.net/), for visualization purposes only; the convex hull for
968 quadrupeds was generated excluding the outlier *Trilophosaurus*. Also plotted are the loading
969 vectors for each anatomical parameter, and silhouettes that illustrate body shapes at the
970 extremes of the bipedal and quadrupedal morphospaces. The enigmatic taxa *Euparkeria* (*E*),
971 *Postosuchus* (*P*) and *Marasuchus* (*M*) are also labelled.
972
973
974 **Figure 4.** Pairwise comparisons of phylogenetically corrected anatomical parameters for
975 both bipeds (solid circles) and quadrupeds (open circles). Where a statistically significant
976 correlation was identified (via major axis regression), the regression line is also plotted;
977 solid line for bipeds, dashed line for quadrupeds. Note that the significant correlation
978 identified between mass and COM_X for bipeds is driven by the residuals for
979 *Heterodontosaurus* (indicated by 'H').
980
981
982 **Figure 5.** Distribution of posterior probabilities obtained for each of the 15 'other' taxa
983 under model 21 LDA across the 1,000 replicates of the Monte Carlo simulation, binned into
984 100 intervals. Red signifies quadruped whereas blue signifies biped. Black vertical lines

985 denote probabilities obtained for each taxon in the main analysis using the original estimates
986 for BM and COM_X.





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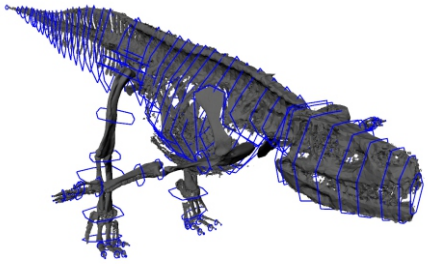

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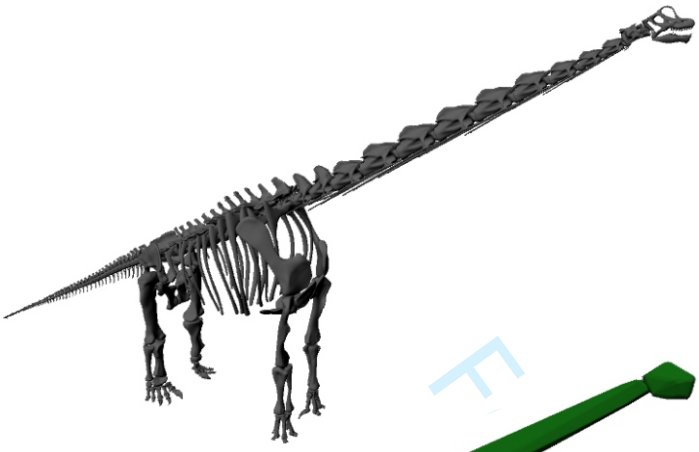

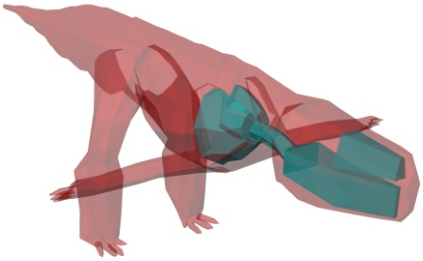

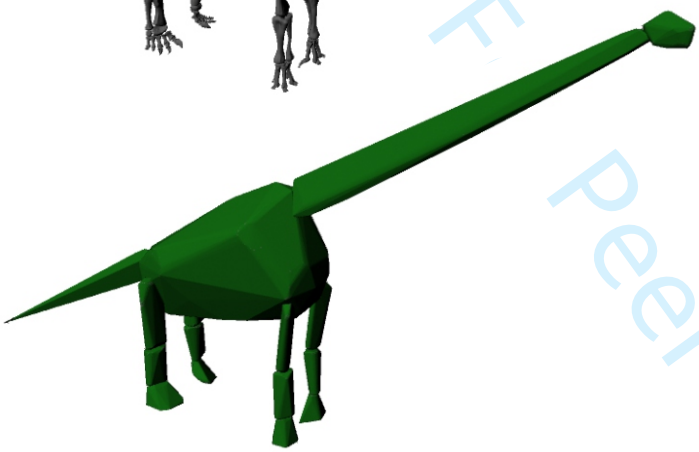

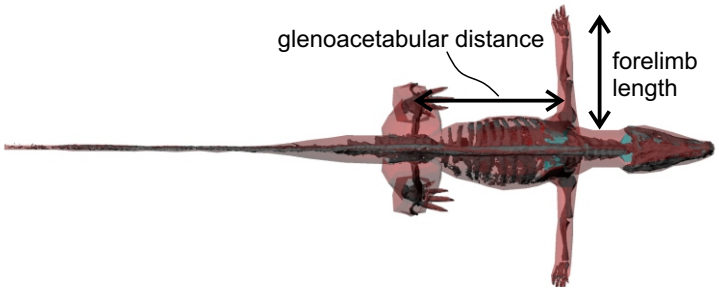

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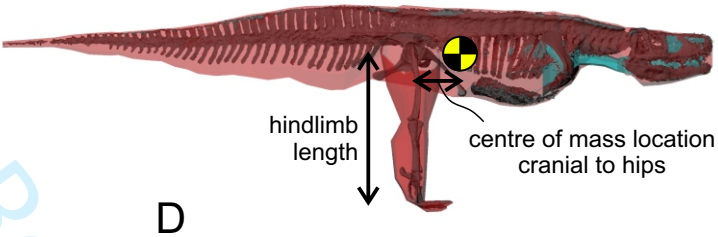

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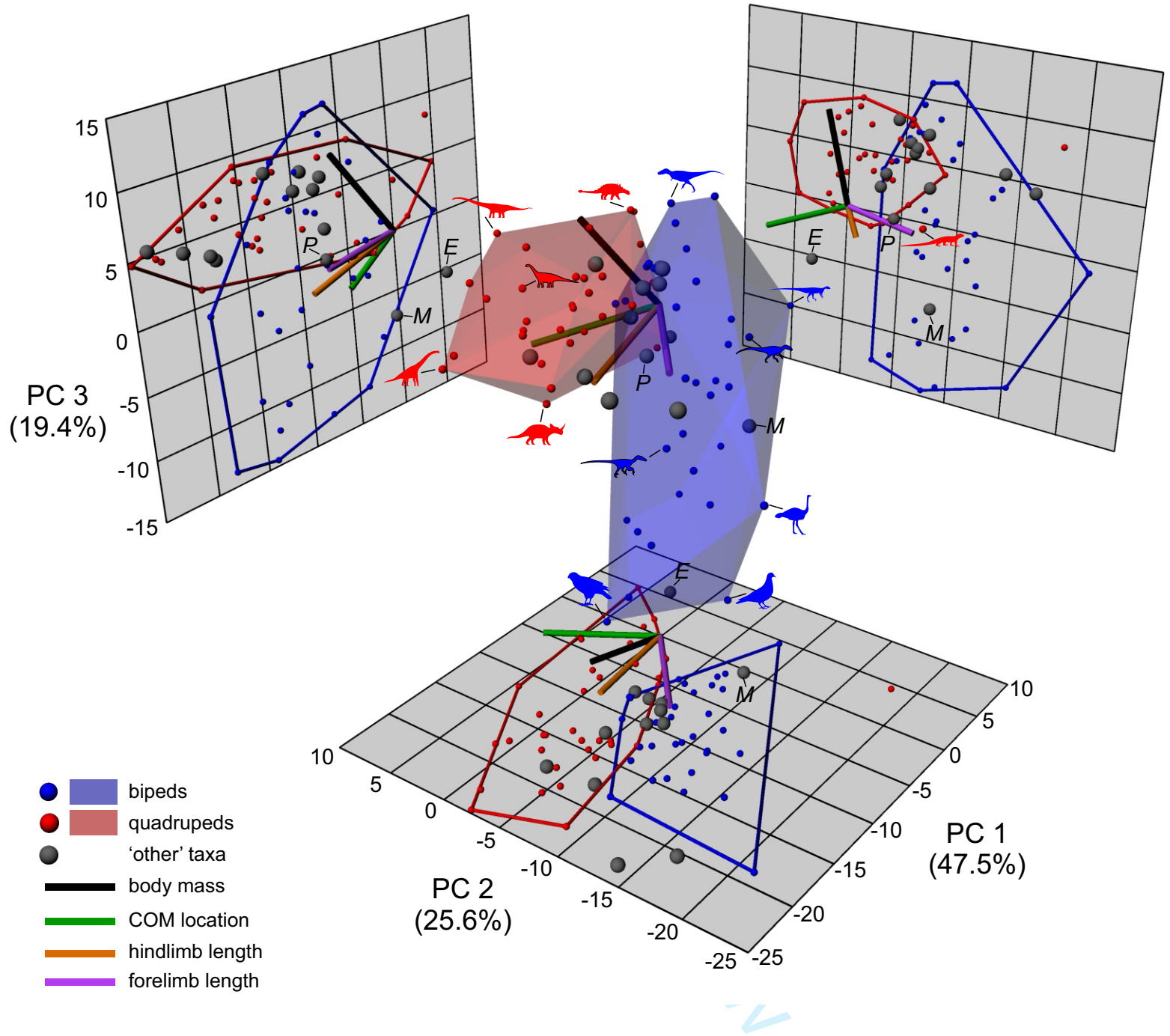
PC 3
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PC 2
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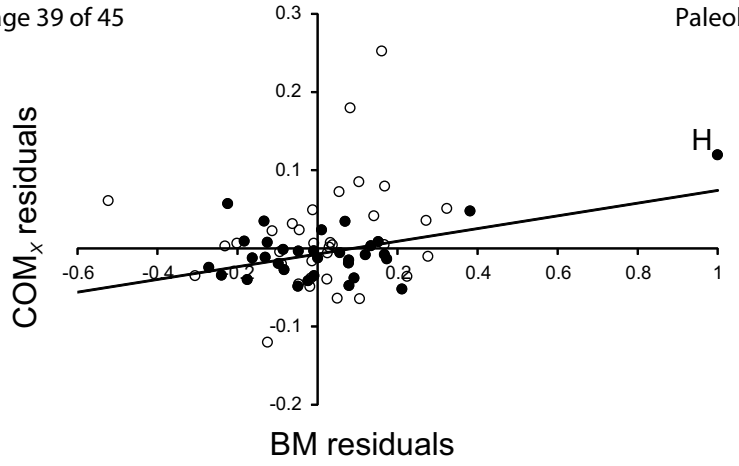
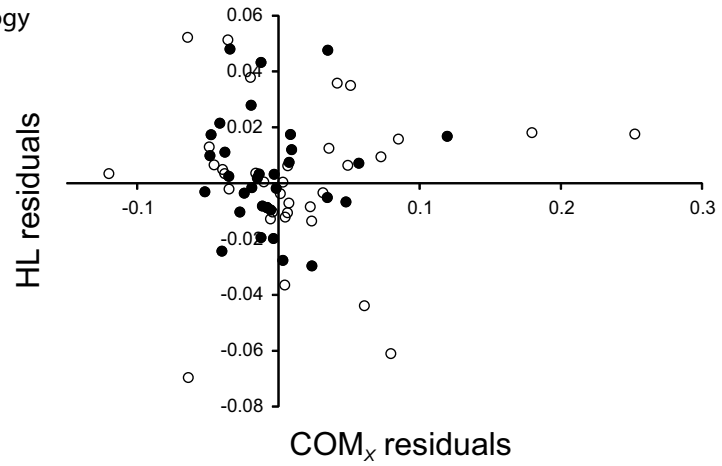
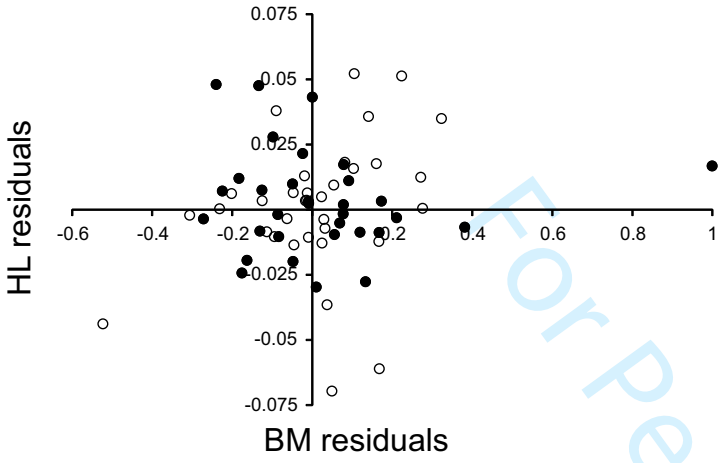
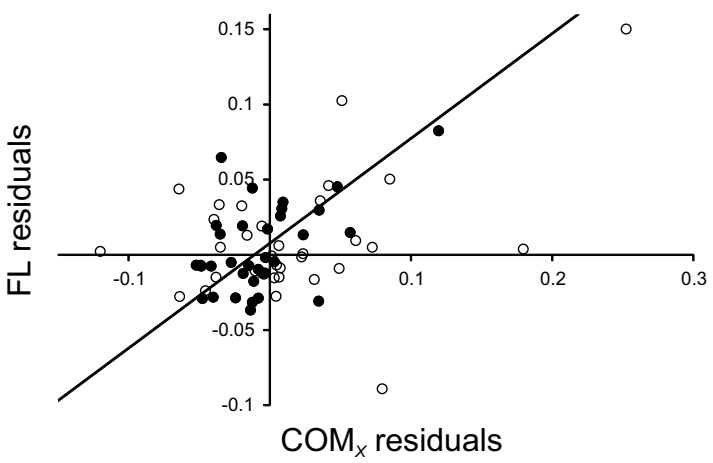
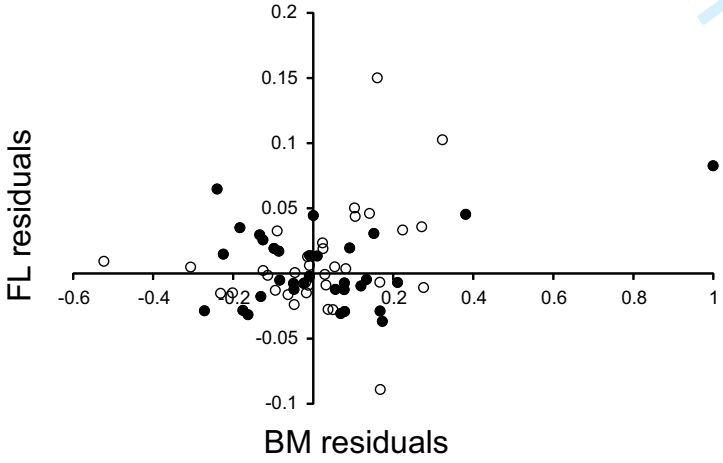
PC 1
(47.5%)
bipeds
quadrupeds
'other' taxa
body mass
COM location
hindlimb length
forelimb length

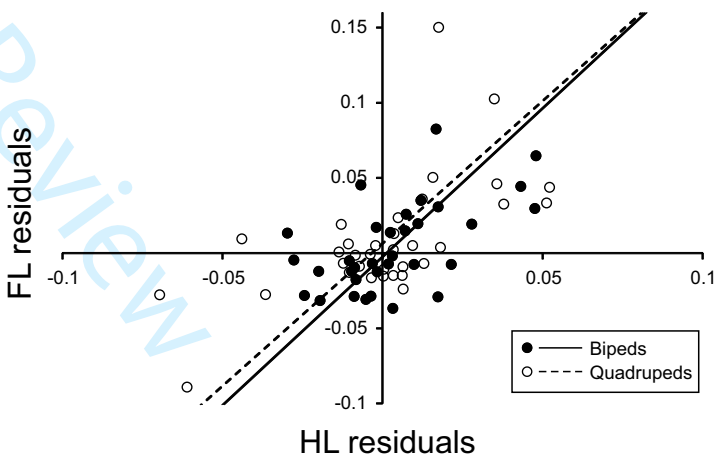












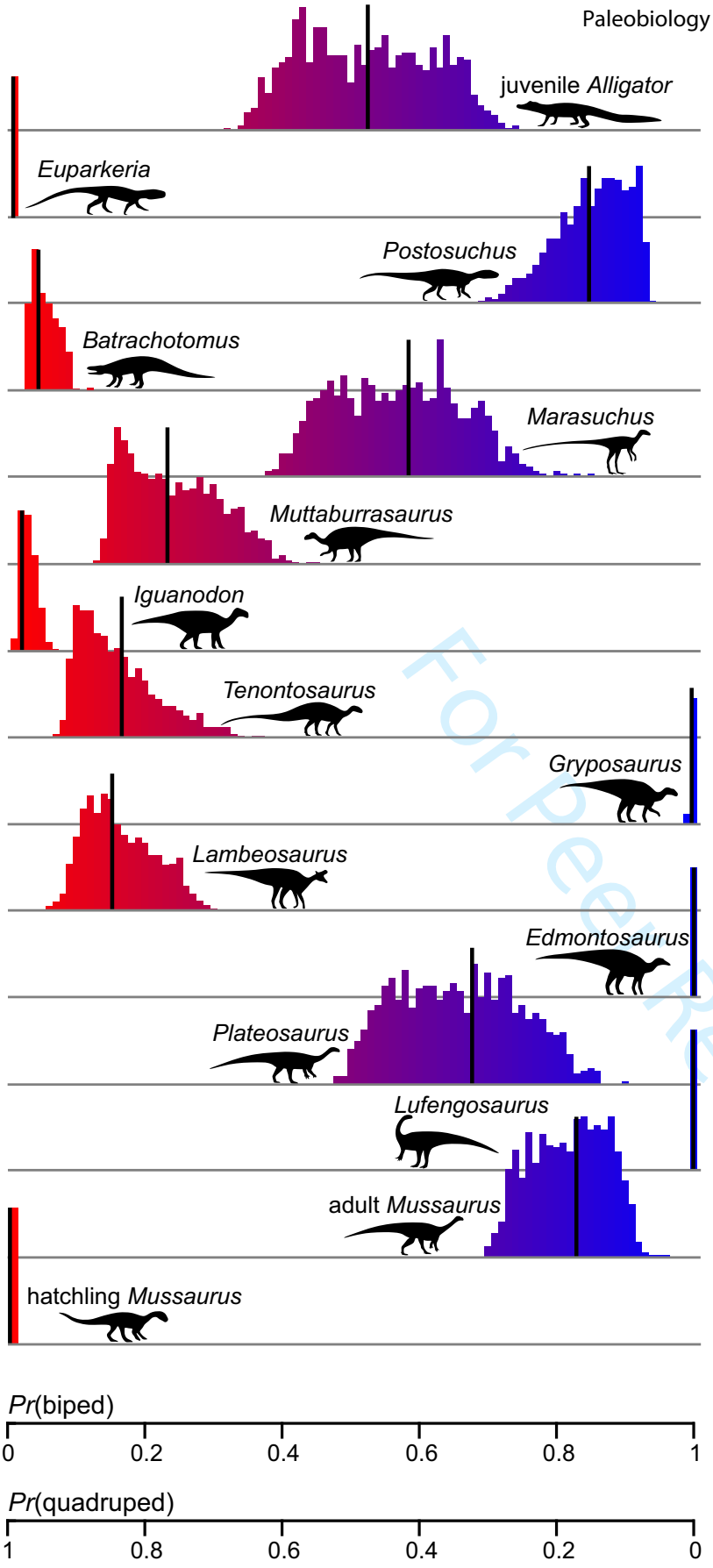


Table 1. Results for comparison between different modelling approaches for size-normalized estimates of mass and centre of mass (mass* and COM*, respectively; see equations 1 and 2), using major-axis regression forced through the origin. Statistically significant results are noted in boldface, indicating systematic bias between modelling approaches; daggers indicate that a significant difference was removed following correction as described in the text. Approaches are listed as ordinate *versus* abscissa in the regressions.

Comparison		*n*	slope	r^2	*F*	*P*
Convex hull v. 3-D slicing	mass*	21	0.878	0.926	4.049	0.0579
	COM*	21	1.49277	0.838	16.638	**0.0006**†
Convex hull v. spline	mass*	13	0.90717	0.988	9.063	**0.0100**
	COM*	13	1.5434	0.857	13.856	**0.0026**†
3-D slicing v. spline	mass*	8	1.10112	0.930	0.742	0.4176
	COM*	8	1.12146	0.841	0.418	0.5387

Table 2. Loadings of each anatomical parameter on the principal components resulting from pPCA.

Parameter	PC1	PC2	PC3	PC4
BM	-0.6	0.2159	0.7703	-0.007
COM_X	-0.5018	0.7722	-0.3286	-0.2097
HL	-0.7139	-0.6108	-0.1052	-0.326
FL	-0.8817	-0.0919	-0.252	0.3881

Table 3. Means (μ) and variances (σ^2) for each PC score, parsed by both locomotor category and major clade.

	PC1		PC2		PC3		PC4	
	μ	σ^2	μ	σ^2	μ	σ^2	μ	σ^2
Bipeds	-8.965	25.205	-8.779	13.496	-0.798	60.747	-5.017	12.648
Quadrupeds	-11.203	60.975	-2.126	19.792	4.525	9.11	-0.248	5.098
Theropoda	-9.983	18.083	-8.961	15.077	-0.74	69.085	-5.375	13.097
Sauropodomorpha	-15.39	21.642	-3.37	12.117	6.279	2.701	-0.549	4.763
Ornithischia	-11.02	56.288	-5.234	19.717	3.203	10.642	-2.153	4.457
Pseudosuchia	-3.887	15.273	-0.96	6.353	0.864	3.819	-1.666	5.262

Table 4. Means and variances for each anatomical parameter, parsed by both locomotor category and major clade. Note that for COM_X, HL and FL, these are the residuals derived from normalizing to body size (GA).

	$\log_{10}$(mass)		COM_X		HL		FL	
	μ	σ^2	μ	σ^2	μ	σ^2	μ	σ^2
Bipeds	1.573	2.366	-0.049	0.034	0.071	0.011	-0.044	0.04
Quadrupeds	3.177	1.155	0.06	0.063	-0.076	0.015	0.047	0.025
Theropoda	1.679	2.598	-0.031	0.033	0.091	0.009	-0.03	0.044
Sauropodomorpha	3.887	0.302	0.062	0.025	-0.009	0.005	0.118	0.019
Ornithischia	2.747	1.276	-0.004	0.037	-0.004	0.02	0.02	0.018
Pseudosuchia	1.772	0.323	0.067	0.004	-0.15	0.01	-0.114	0.006

Table 5. Results for pairwise comparison of the phylogenetically-corrected values for each anatomical parameter by MA regression. Statistically significant results are noted in boldface.

	bipeds			quadrupeds			slope test, bipeds v. quadrupeds	
	slope	r^2	***P***	**slope**	r^2	***P***	***t***	***P***
COM_X v. BM	0.0814	0.2691	**0.002***	0.098	0.0422	0.2441	0.0368	0.8479
HL v. BM	-0.0034	0.0015	0.8281	0.049	0.0937	0.0784	2.7236	0.0989
FL v. BM	0.0414	0.1007	0.0719	0.0749	0.0908	0.0834	0.4912	0.4834
HL v. COM_X	0.0113	0.0002	0.9382	0.013	0.0008	0.8731	0.0001	0.9917
FL v. COM_X	0.6976	0.2497	**0.0031**	0.3259	0.1677	0.0162	2.315	0.1281
FL v. HL	1.9758	0.3222	**0.0006**	1.8966	0.3812	**0.0001**	0.0139	0.9061

*When *Heterodontosaurus* is removed from consideration, the correlation degenerates to becoming non-significant (cf. Fig. 4)

Table 6. Classifications and posterior probabilities (*Pr*) resulting from LDA applied to the 15 'other' taxa, for the four best-performing models. The correct classification rate on the training dataset is also given for each model.

	Model 11 (98.48%)		**Model 20 (98.28%)**		**Model 21 (100%)**		**Model 22 (98.28%)**	
Taxon	**Prediction**	***Pr***	**Prediction**	***Pr***	**Prediction**	***Pr***	**Prediction**	***Pr***
Euparkeria	quadruped	0.562	quadruped	0.821	quadruped	0.999	quadruped	0.981
Batrachotomus	quadruped	0.884	quadruped	0.941	quadruped	0.955	quadruped	0.959
Postosuchus	biped	0.984	biped	0.995	biped	0.847	biped	0.981
Alligator (juvenile)	biped	0.94	biped	0.898	biped	0.525	biped	0.919
Marasuchus	biped	0.999	biped	0.993	biped	0.584	biped	0.998
Muttaburrasaurus	quadruped	0.987	quadruped	0.986	quadruped	0.767	quadruped	0.981
Tenontosaurus	quadruped	0.973	quadruped	0.995	quadruped	0.834	quadruped	0.962
Iguanodon	quadruped	0.975	quadruped	0.958	quadruped	0.979	quadruped	0.995
Lambeosaurus	quadruped	0.823	quadruped	0.893	quadruped	0.848	quadruped	0.902
Gryposaurus	biped	0.985	biped	0.944	biped	0.997	biped	0.999
Edmontosaurus	biped	0.999	biped	1	biped	1	biped	1
Plateosaurus	quadruped	0.696	quadruped	0.791	biped	0.677	biped	0.504
Lufengosaurus	biped	0.982	biped	0.998	biped	0.999	biped	0.999
Mussaurus (adult)	quadruped	0.583	quadruped	0.541	biped	0.829	biped	0.676
Mussaurus hatchling)	biped	0.953	biped	0.738	quadruped	0.997	quadruped	0.637